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ABSTRACT

Action spectra of UV damage to plants must be used as weighting functions to (1) evaluate the relative increase of solar UV radiation that would result from a decreased atmospheric ozone layer, the radiation amplification factor--RAF, (2) evaluate the existing natural gradients of solar UV irradiance on the earth, and (3) compare UV radiation from lamp systems in experiments with solar UV radiation in nature. Only if the relevant biological action spectra have certain characteristics is there a potential biological problem that would result from ozone reduction. Similarly the existence of a natural latitudinal solar UV gradient is dependent on action spectrum characteristics.

Several UV action spectra associated with different basic modes of damage to plant tissues all have the common characteristic of decreasing effect with increasing wavelength; however, the rate of decline varies considerably. Extrapolation from action spectra that have been measured on isolated organelles and microorganisms using monochromatic radiation to effects of polychromatic radiation on intact higher plants is precarious. Development of action spectra using polychromatic radiation and intact higher plant organs can yield spectra that are of more ecological relevance for weighting factors in assessment of the ozone reduction problem. An example of an action spectrum for photosynthetic inhibition developed with polychromatic radiation is provided in this chapter. This action spectrum has different characteristics, and results in a greater RAF than do action spectra for inhibition of a partial photosynthetic reaction, the Hill reaction, developed with isolated chloroplasts and photosynthetic bacteria. Circumstantial evidence from experiments with plants originating from different latitudes also supports the notion that action spectra with characteristics similar to that of the provisional spectrum, developed with polychromatic radiation, are appropriate. Further work with polychromatic radiation is encouraged.

There are two basic types of error that are associated with the use of action spectra in biological assessments of the ozone reduction problem, the RAF errors and the enhancement errors. The former are those associated with calculation of the RAF, and the latter are those derived from calculation of the UV radiation enhancement used in experiments with lamp systems. While the RAF errors are recognized, the enhancement errors have not been generally appreciated. An error analysis is presented showing that the enhancement errors will typically be larger and in the opposite direction

than the RAF errors. The enhancement error should be considerably less in field UV supplementation experiments than in most laboratory experiments which employ fluorescent lamps as the primary UV-B radiation source.

INTRODUCTION

Traditionally, biological action spectra have been employed to elucidate photobiological mechanisms, and specifically to identify potential chromophores. Action spectra are usually assessed by evaluating biological responsiveness to monochromatic irradiation. In order to identify potential chromophores, there has been an emphasis on the fine structure of action spectra and little attention has been directed to the tails of these spectra.

In assessment of the consequences of solar UV-B radiation changes, action spectra serve a very different role. Weighting functions are derived from action spectra to assess the relative biological effectiveness of polychromatic irradiance. Spectral irradiance is weighted and then integrated over a waveband of interest, thus:

$$\text{effective irradiance} = \int I_\lambda \, E_\lambda \, d_\lambda \qquad (1)$$

where I_λ is the spectral irradiance, and E_λ is the relative effectiveness of irradiance at wavelength λ to elicit a particular biological response. The limits of the integration are prescribed by the wavelengths where either I_λ or E_λ approach zero.

Spectral irradiance and the action spectra can be expressed on either a photon or an energy basis. As units of effective irradiance it is most useful to speak of "weighted" or "effective" energy flux or photon flux density (e.g., effective W m^{-2} or effective moles photons m^{-2} s^{-1}) and, of course, to specify the action spectrum used as a weighting function and the wavelength to which the spectrum is normalized. Special units analogous to units of illumination (e.g., lux) have been previously devised for effective UV radiation (such as sunburn units, E-viton and the Finsen for erythemally effective radiation (Robertson 1975; Luckiesh and Holladay 1933) and the G-viton for germicidal UV radiation (Luckiesh and Holladay 1933). However, unlike illumination where a standard spectral luminosity function has been well accepted, UV action spectra for various biological phenomena are continually being refined or abandoned in favor of new action spectra and, thus, either the units need to be redefined or new units described. Therefore, use of effective energy or photon flux with a specified action spectrum is quite preferable to the definition of new units.

The utility of weighting the UV irradiance and, thus, expressing biologically effective irradiance for the ozone reduction problem derives from the highly wavelength-specific absorption characteristics of atmospheric ozone and the wavelength specificity of biological action spectra in the UV-B waveband (National Academy of Sciences 1979; Caldwell 1981; Nachtwey and Rundel 1982). The expression of weighted effective irradiance is useful in addressing three basic issues:

(1) The degree to which biologically damaging solar UV irradiation is increased when atmospheric ozone decreases is very dependent on the action spectrum characteristics. The increment of biologically damaging solar irradiation resulting from a given level of ozone reduction for a specific set of conditions, is known as the radiation amplification factor, RAF (National Academy of Sciences 1979). Without calculation of a RAF, which takes the biological effectiveness of each wavelength into account, the increment of total solar UV-B flux resulting from ozone reduction is trivial, e.g., 1% increase of UV-B radiation for 16% ozone reduction for midday irradiance in the summer at temperate latitudes (Caldwell 1981). The increase of solar UV-B irradiation as a function of ozone reduction only becomes significant when the biological effectiveness of this radiation is calculated and the action spectrum for this calculation has certain characteristics. By the same token, if the action spectrum of a particular biological phenomenon does not exhibit the appropriate characteristics, the RAF will be very small and this phenomenon can be eliminated from concern with respect to the consequences of ozone reduction without the necessity of dose-response studies.

(2) The steepness of the natural latitudinal gradient of solar UV-B irradiance that currently exists on the earth's surface should also be evaluated in terms of potential biological effectiveness. The natural gradient of UV-B radiation serves as a basis for study of organism response to solar UV-B radiation and can provide insight into potential consequences of ozone reduction. This gradient has been used most frequently in the analysis of human skin cancer incidence; however, study of plant adaptation to UV-B radiation at different latitudes can also be instructive (e.g., Caldwell et al. 1982; Robberecht et al. 1980). As is the case with ozone reduction, without taking biological effectiveness of solar UV-B irradiation into account, the natural latitudinal gradient of solar UV-B radiation is virtually nonexistent (Caldwell 1981).

(3) Since spectral irradiance received from commonly-used lamp systems for UV-B studies does not match that of solar irradiance, it is only possible to draw comparisons by calculating "biologically effective" radiation using action spectra as weighting functions. Characteristics of action spectra will thus dictate the amount of radiant flux delivered by lamp systems in experiments designed to evaluate potential consequences of ozone reduction under different conditions.

This chapter will (1) review a few action spectra illustrating different fundamental mechanisms of UV-B damage in plant cells, (2) discuss the use of polychromatic radiation in determining action spectra and illustrate this with a new action spectrum for photosynthetic inhibition, (3) show the nature of radiation amplification factors that result from action spectra of different characteristics, (4) briefly discuss the implications of action spectra for the natural latitudinal gradient of solar UV-B radiation, and (5) develop an error analysis of the types and magnitude of errors that might be encountered in biological assessments by assuming an improper action spectrum.

ANALYSIS

Modes of Damage and Their Spectra

Ultraviolet radiation can damage plant cells by several basic mechanisms and these pathways of damage likely involve several different chromophores. To illustrate the diversity of damage pathways, several action spectra are depicted in Fig. 1. In each case the reaction is identified with damage to a specific entity or process in the cell. However, this does not mean that the entity damaged is necessarily the primary chromophore (Peak and Peak 1983). All spectra are normalized to 300 nm. Though these spectra

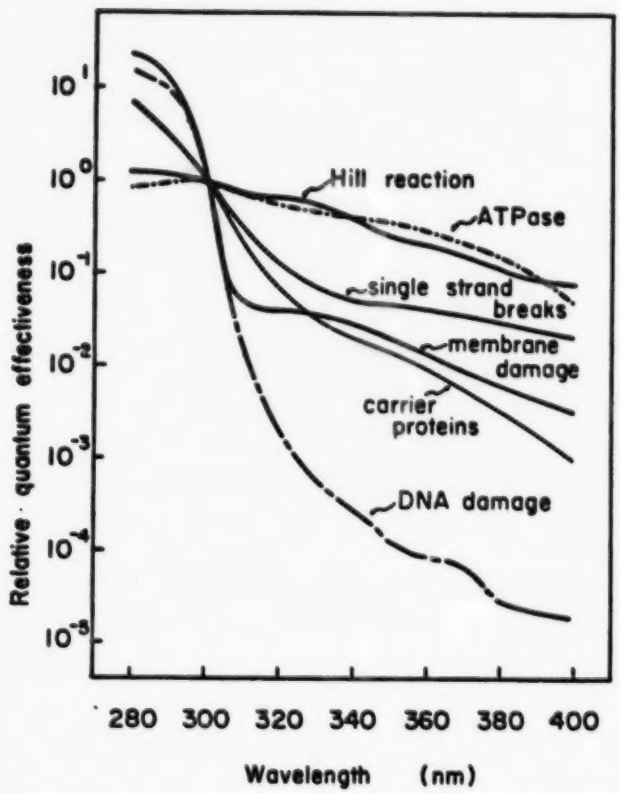

Fig. 1. Ultraviolet action spectra representing basic modes of damage to plant tissues. The spectra were all developed with monochromatic radiation and are plotted on a quantum effectiveness basis relative to 300 nm. These include inhibition of Hill reaction activity in isolated chloroplasts of spinach (Jones and Kok 1966), inhibition of adenosine triphosphatase (ATPase) from plasma membranes of Rosa damascena (Imbrie and Murphy 1982), induction of single strand breaks of Bacillus subtilis DNA (Peak and Peak 1982), lethality of stationary phase cells of E. coli associated with cell membrane damage (Kelland et al. 1983), inhibition of alanine uptake in E. coli linked to inactivation of carrier proteins (Sharma and Jagger 1981), and inactivation of stationary phase cells in E. coli associated with nucleic acid damage (Webb 1977).

represent different basic pathways of damage, and in many cases presumably very different chromophores, all have the common property of decreasing effect as wavelength increases. These spectra have been developed in the normal manner using monochromatic radiation and in several cases have been pursued through several orders of magnitude. If these were to be plotted with a linear ordinate, the differences in these spectra would be much less apparent. Nevertheless, as will be discussed subsequently, if these spectra are to be used as weighting factors for solar UV radiation, which increases by orders of magnitude with increasing wavelength, the differences in slopes of these action spectra are of key importance. These spectra have been determined with isolated organelles, membranes, or microorganisms, but none involved intact higher plants.

Complications: Intact Higher Plants and Polychromatic Radiation

Since the spectra illustrated in Fig. 1 differ greatly in their decline with increasing wavelength, it is important to know which of these primary damage mechanisms are the most important for intact higher plants exposed to solar radiation. This is not an easily answered question. One would need to know (1) the basic sensitivity of the respective targets (e.g., DNA, membranes, photosystem II of photosynthesis, etc.) for the higher plant species in question, (2) how well shielded these targets are within the plant organ (i.e., the effective spectral fluence reaching the target), (3) to what extent reciprocity would apply, and (4) if radiation at different wavelengths when applied simultaneously and in proportion to their occurrence in sunlight would have strictly additive effects, as predicted by the action spectrum, or whether these effects would be positively or negatively synergistic. Addressing these several issues is hardly a trivial undertaking and satisfactory answers are not likely to be quickly forthcoming. For example, as to the question of synergistic effects of radiation at different wavelengths, much is known about mechanisms of UV radiation effects on nucleic acids and yet it is still difficult to quantitatively predict synergistic effects in higher plants. From *in vitro* studies and from *in vivo* experiments with microorganisms, it is clear that there are qualitative differences between UV-B and UV-A damaging photoreactions (Peak and Peak 1983): UV-A radiation can drive photorepair of UV-B-induced damage (Jagger 1981), UV-B radiation can induce other repair systems which can repair at least a fraction of the UV damage (Menezes and Tyrrell 1982), UV-A radiation can cause growth delay in bacteria which allows more time for dark repair systems to operate (Jagger 1981), and, finally, UV radiation at high fluence rates can damage UV repair systems (Webb 1977). The net effect of these phenomena and their applicability to higher plant nucleic acid damage is not easily envisaged.

The primary site of UV damage to photosynthesis is in the reaction center of photosystem II (Renger et al., this volume; Noorudeen and Kulandaivelu 1982) and most likely does not involve nucleic acids. For intact higher plants, interactions between UV-B and longer wavelength radiation have been frequently reported though the mechanisms are not understood. Plant leaves which have developed under low visible radiation conditions are considerably more sensitive to UV-B inhibition of photosynthesis (Teramura et al. 1980; Sisson and Caldwell 1976; Warner and Caldwell 1983). Yet, there is also some evidence that higher visible irradiance during UV-B irradiation increases the inhibition of photosynthesis even though the visible irradiation by itself is not sufficient to inhibit photosynthesis (Warner

and Caldwell 1983). At present, one can only speculate about the mechanisms involved in these interactions.

A Photosynthetic Inhibition Spectrum

Predicting the net effect of interactions between radiation of different wavelengths for phenomena such as nucleic acid damage or inhibition of photosynthesis is not possible at present even though the action spectra for some repair processes such as photoreactivation are known. Thus, in order to account for the synergistic effects of radiation at different wavelengths when "damage" action spectra are to be used as weighting functions for polychromatic radiation, one is forced to take a more empirical approach. This can be done by employing polychromatic radiation in the development of action spectra and using intact plant organs. In this process the biological responses to different combinations of polychromatic irradiation are determined and these responses and associated spectral irradiance data can be deconvoluted to yield an action spectrum (Rundel 1983). With respect to the ozone reduction problem, the most logical combinations of polychromatic irradiation involve a constant background of longwave UV-A and visible irradiance with increments of radiation at shorter wavelength intervals. This process can sacrifice some of the fine structure of an action spectrum, but this is of less concern for the purpose of weighting functions.

This series of polychromatic irradiation distributions should be planned to account for the tail of the action spectrum into the UV-A or visible waveband, as the case may be. Characteristics of the action spectrum below 280 nm are of no concern with respect to solar UV radiation changes because of the effectiveness of atmospheric ozone absorption, even in the case of a severely depleted ozone layer (Caldwell 1979). Yet, if a particular lamp system emits shorter wavelengths, the weighting function should include these as well.

To illustrate this polychromatic approach to action spectrum development, reduction of photosynthesis of an intact leaf of Rumex patientia will be depicted. Photosynthetic inhibition of higher plants by UV radiation is of potential concern with respect to ozone reduction. For some species under certain experimental conditions, solar UV radiation at flux rates now received at temperate latitudes has been shown to reduce photosynthesis (Bogenrieder and Klein 1977; Sisson and Caldwell 1977). Yet to be resolved, however, is the extent to which plants experience photosynthetic inhibition under field conditions, or how much they might be inhibited in the event of ozone layer reduction. Nevertheless, there is sufficient impetus to select net photosynthesis for action spectrum analysis because of its potential susceptibility to solar UV radiation and its obvious importance for plant biology. Furthermore, net photosynthesis is an integrated physiological process which requires the integrity of membrane systems and the coordinated action of photochemical and enzymatic processes. Thus, it also serves as a useful indicator of plant response to stress.

Methods: Assessment of photosynthetic depression resulting from UV irradiation involved the determination of net CO_2 uptake by plant leaves, exposure of the leaves to a particular polychromatic irradiation distribution, and then subsequent determination of CO_2 uptake capacity under identical conditions. Ideally, the leaves would be exposed to the inactivating

UV irradiation over a period of several days or weeks as would occur under field conditions. Unfortunately, this involves unreasonable biological and experimental complications. Leaf photosynthetic characteristics change appreciably with leaf age (e.g., Sestak 1977; Sisson and Caldwell 1977). These changes combined with the time and logistic requirements for such experiments render this approach infeasible. Thus, the irradiation periods ranged from one to 16 hours. Seven polychromatic radiation distributions were employed. For each, a dose-response relationship was developed. Even with these irradiation periods, such experiments are very time consuming.

The spectral irradiance for the seven polychromatic irradiation distributions are shown in Fig. 2. These were developed by using a 2.5-kW xenon high pressure lamp and a combination of dichroic and sharp cutoff filters. Much of the visible and infrared radiation was removed by the dichroic filter arrangement in order to prevent excessive leaf temperatures. Yet, there was sufficient visible flux (400 μmoles m^{-2} s^{-1} between 400 and 700 nm) to drive photosynthesis of the plants during the UV irradiation. Leaves still intact with the remainder of the plant were placed on a slowly revolving stage in this radiation field to insure even irradiation of the leaves.

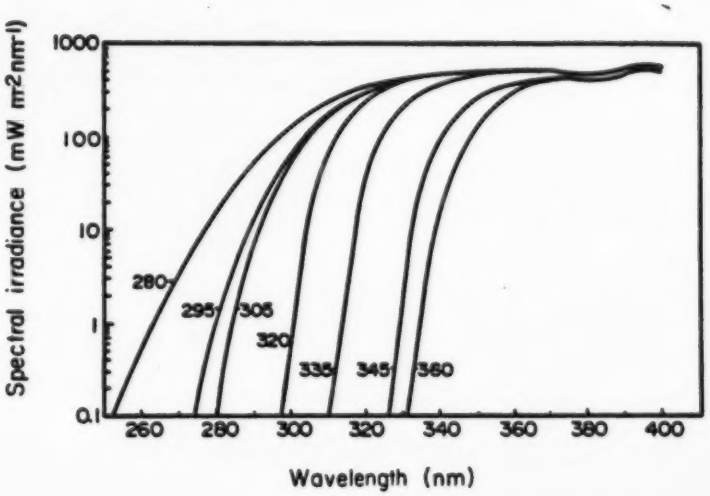

Fig. 2. Spectral irradiance for seven polychromatic irradiation distributions used in the development of an action spectrum for inhibition of photosynthesis. Radiation is supplied by a 2.5-kW xenon high pressure lamp and filtered with a combination of dichroic and absorption filters. The sharp cutoff filters used for each distribution are from the Schott WG series.

Net photosynthetic rates of intact leaves were assessed by measurements of net CO_2 uptake under specific environmental conditions in a gas exchange cuvette. By measurement of simultaneous CO_2 and water vapor flux of the foliage as well as other parameters including leaf temperature, CO_2 concentration in the cuvette air, and water vapor concentration in the cuvette, it is possible to calculate intercellular CO_2 concentrations within the

leaf (e.g., Caldwell et al. 1977). Intercellular CO_2 is influenced primarily by photosynthetic rates, CO_2 in the cuvette airstream, and diffusion resistance provided by stomata. Since photosynthesis is normally substrate limited, it is important to manage the cuvette conditions to maintain a constant intercellular CO_2 concentration in the leaf before and after irradiation so that metabolic photosynthetic capacity of a leaf is assessed without the complication of changes in diffusion resistances between the leaf intercellular CO_2 and the air. Direct coupling of the gas exchange system with a computer allows immediate assessment of these parameters so that adjustments in cuvette conditions can be made during the course of these measurements.

Results and discussion: The dose-response relationships for net photosynthetic inhibition of Rumex patientia leaves are shown in Fig. 3 for the different spectral irradiance distributions. Each data point represents a different leaf measured on a different date since each determination required a day to complete. Nevertheless, these dose-response data reveal linear relationships. The coefficients of determination, r^2, range between 0.63 and 0.98 with an average of 0.87. The spectral irradiance combination which included the least short wavelength radiation (WG 360, Fig. 2) did not result in inhibition of photosynthesis under these conditions even after 16 hours of exposure.

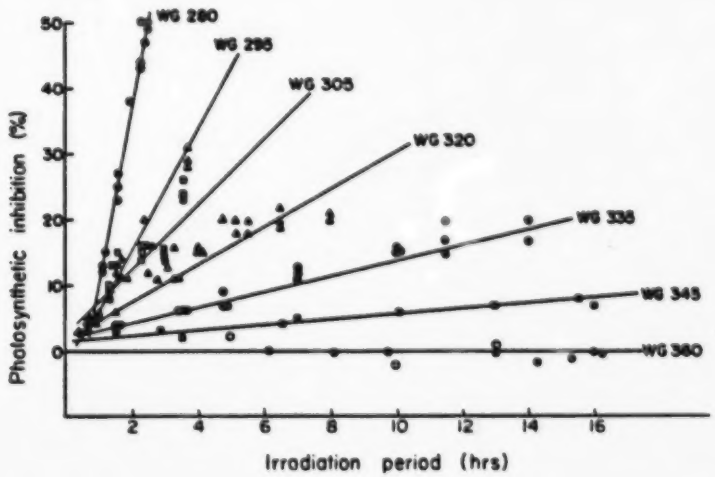

Fig. 3. Relative inhibition of net photosynthesis of intact Rumex patientia leaves exposed to the polychromatic irradiation combinations shown in Fig. 2.

These photosynthetic inhibition data indicate that when there was sensitivity to a particular irradiation distribution, we were dealing with a linear portion of the dose-response relationship. This is important in developing action spectra. If a particular dose-response relationship exhibits diminished slope as with saturation, these data cannot be compared with a dose-response relationship which is in the initial, linear phase. The dose-response relationships presented here indicate that it is suitable

to utilize the slope of these linear regression relationships for biological response in developing these action spectra.

When these slopes are taken as the relative effect for each spectral irradiance combination, an action spectrum can be deconvoluted from the slopes and respective spectral irradiance data (Rundel 1983). Several possible spectra can result depending on the exact procedure followed. The spectrum shown in Fig. 4 is the monotonic function that provided the best fit to the data (Rundel 1983).

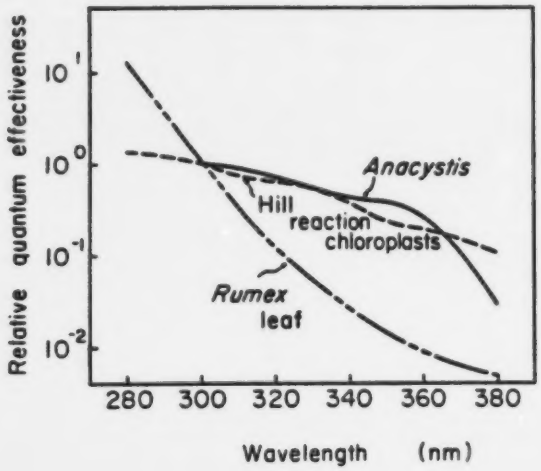

Fig. 4. Action spectrum for inhibition of photosynthesis for an intact leaf of Rumex patientia deconvoluted from the data of Figs. 2 and 3 by Rundel (1983) for his monotonic function that provided the best fit. Spectra for inhibition of Hill reaction in isolated spinach chloroplasts (Jones and Kok 1966) and of the Cyanobacterium, Anacystis, (Hirosawa and Miyachi 1983) are also shown. The two Hill reaction spectra were developed with monochromatic radiation.

The action spectrum deconvoluted from the polychromatic radiation study with intact leaves is considerably steeper than the spectrum for inhibition of a partial photosynthetic reaction, the Hill reaction, conducted by treating isolated spinach chloroplasts with monochromatic radiation (Jones and Kok 1966). The spectrum for inhibition of fluorescence rise time from spinach thylakoid suspensions (Björn et al. in this volume) and a spectrum for Hill reaction inhibition of the Cyanobacterium, Anacystis nidulans, (Hirosawa and Miyachi 1983), also developed with monochromatic radiation, correspond closely with the spectrum of Jones and Kok. The two Hill reaction inhibition spectra are also shown in Fig. 4.

Preliminary results of more recent action spectrum studies for Rumex patientia and other species suggest that the action spectrum may exhibit steeper declines with increasing wavelength than the spectrum for Rumex shown in Fig. 4. This new work involves simultaneous UV irradiation and leaf gas exchange measurements. With a split-beam arrangement, the leaf is

also simultaneously receiving high visible irradiation (800 to 1200 μmoles m^{-2} s^{-1}, depending on the species being investigated). Though the visible flux employed is still only 40 to 60 percent of that in midday solar radiation, photosynthesis is light saturated. Since subsequent action spectra conducted with higher visible irradiance may reveal steeper declines with increasing wavelength, the action spectrum shown in Fig. 4 for Rumex should be considered as only provisional. The importance of the rate of decline with increasing wavelength when action spectra are used as weighting functions is discussed in a subsequent section.

Although practical limitations do not permit these experiments to be performed with spectral irradiance that exactly matches that of solar radiation, this approach with polychromatic radiation and intact leaves should provide a much more realistic approximation of the ecologically relevant action spectra for photosynthetic inhibition. It also indicates that extrapolation from damage spectra of specific physiological reactions, as shown in Fig. 1, to intact organisms may not provide reliable results. As will be discussed in a subsequent section, there is also indirect evidence that the action spectrum developed for inhibition of photosynthesis by this polychromatic approach may be appropriate for plants in nature.

Action Spectra and Radiation Amplification Factors

One of the functions of action spectra in assessment of the ozone reduction problem is their use in evaluating radiation amplification factors, RAF, i.e., the relative increase in biologically effective UV radiation for a given level of ozone reduction. As noted in a previous section, all UV damage spectra exhibit a general decrease in effectiveness with increasing wavelength, though the rates of decline vary considerably (e.g., Fig. 1). Since solar spectral irradiance increases by orders of magnitude with increasing wavelength, the rate of decline of action spectra has a pronounced effect on the resulting RAF when these spectra are used as weighting functions. Furthermore, even though ozone reduction would only result in increases of solar spectral irradiance in the UV-B part of the spectrum (Caldwell 1981), the weighting function should include all wavelengths of the solar spectrum where the weighted spectral irradiance adds appreciably to the integral of Eq. (1). Although many UV-B biological damage spectra include the UV-A region, few extend far into the visible spectrum. This is not of great consequence if the effectiveness is already so low by 400 nm that the weighted visible flux would not contribute significantly to the total biologically effective flux (such as is the case for DNA damage), or if the action spectrum is already sufficiently flat so as to result in a negligible RAF (as is the case for the Hill reaction spectrum).

To illustrate the behavior of the RAF calculated with different action spectra, a variety of spectra currently in use, as well as the provisional photosynthetic inhibition action spectrum for Rumex, are portrayed in Fig. 5 and the respective RAF values for different total ozone column thickness relative to 0.32 cm in Fig. 6. The model of Green et al. (1980) was used to calculate the spectral irradiance. The action spectra have been chosen because they illustrate the RAF values for spectra with a broad range of slopes.

The DNA damage spectrum is a generalized spectrum compiled by Setlow (1974). The generalized plant damage spectrum is also the result of a compilation of several plant damage spectra that exhibit similar characteristics (Caldwell 1971). The generalized plant damage spectrum terminates at 313.3 nm simply because that was the longest wavelength (an emission line from mercury vapor UV lamps) where information was available for these spectra at the time they were compiled. (If these spectra decline steeply beyond 313 nm as the DNA-damage spectrum does, the contribution of weighted spectral irradiance at wavelengths greater than 313 nm would be negligible for the total integrated biologically effective flux.) The Robertson-Berger, R-B, meter is a widely used integrating dosimeter for solar UV monitoring (Berger et al. 1975). The spectral response of this meter was originally designed to approximate that of human skin erythema. The provisional spectrum for photosynthetic inhibition of Rumex (Fig. 4) is also included; although preliminary data (cited previously) indicate that a steeper spectrum may be more appropriate and that this would result in greater RAF values.

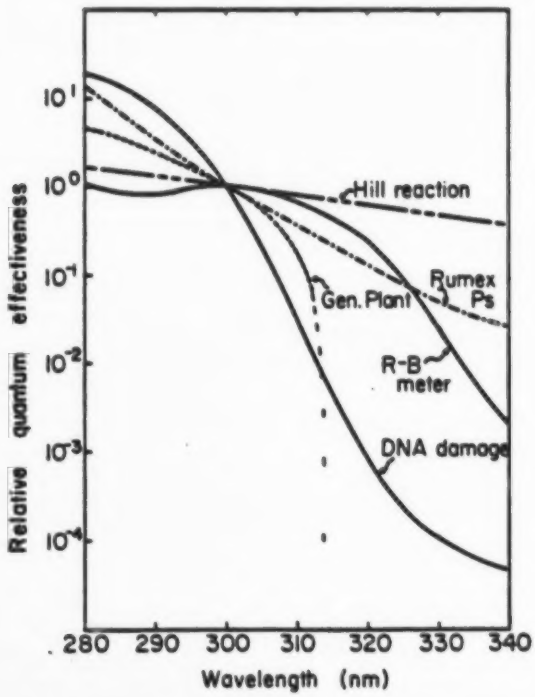

Fig. 5. Action spectra exhibiting different rates of decline with increasing wavelength. These include the spectrum for Hill reaction inhibition of spinach chloroplasts (Jones and Kok 1966), the Rumex leaf photosynthesis inhibition spectrum (Fig. 4), a spectrum for the Robertson-Berger meter (Robertson 1975), a generalized plant damage spectrum (Caldwell 1971) and a generalized DNA damage spectrum (Setlow 1974).

The RAF values in Fig. 6 are calculated over the waveband 290-380 nm. For the DNA and generalized plant damage spectra there would be no significant effect if the integral included longer wavelengths. For the Hill reaction

and R-B meter spectra, the RAF values would be even smaller if longer wavelengths were included in the integration. The deconvoluted Rumex spectrum is unreliable at longer wavelengths. As noted in the previous section, polychromatic irradiation which did not include wavelengths shorter than 330 nm had no effect on photosynthesis (Figs. 2 and 3). Also shown in Fig. 6 is a slope indicating a 2% increase of biologically damaging radiation for each 1% decrease of ozone column thickness which has commonly been used as a guideline for the RAF (National Academy of Sciences 1979).

Radiation amplification factors are dependent on the degree of ozone reduction and this dependency is more pronounced for steeper action spectra (Fig. 6). The RAF is also quite dependent on solar angle and, thus, RAF values appropriate for total daily effective radiation would be an integrated function for different times of day. The daily RAF would be dependent on latitude and time of year (National Academy of Sciences 1979). The RAF values in Fig. 6 are plotted for a solar angle from the zenith of 33.6° (air mass of 1.2). For the summer solstice at 40° latitude, these RAF values would also be approximately the same as total integrated daily dose RAF values.

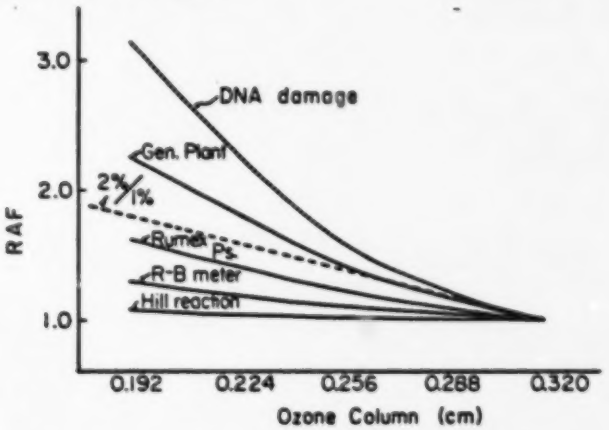

Fig. 6. Radiation amplification factors calculated for different ozone column thickness, relative to 0.32 cm, and a solar angle from the zenith of 33.6° calculated according to the action spectra shown in Fig. 5. The dashed line represents a case of 2% increase in biologically effective radiation for a 1% decrease of ozone. The model of Green et al. (1980) was used to calculate the solar spectral irradiance (direct beam + diffuse) used for those RAF values.

The Natural Latitudinal Gradient of Solar UV-B Radiation

Natural latitudinal gradients of solar UV-B radiation exist on the earth. This is primarily the result of differences in prevailing solar angles and total ozone column thickness at different latitudes (Caldwell 1981). Correlations between the latitudinal UV-B gradient and skin cancer incidence of selected human populations have been used as a tool to predict increases of skin cancer as a function of ozone reduction (e.g., National Academy of Sciences 1979). An analogous correlation between latitude and changes in crop yield or other nonhuman biological phenomena are too confounded with other environmental variables such as soils, temperature

and moisture to be of use in predicting the consequences of ozone reduction. Nevertheless, controlled study of plant response to, and tolerance of, UV-B irradiation by species from different latitudes can provide some useful insight as to how plants cope with different levels of UV-B irradiation. However, just as the magnitude of solar UV-B increase resulting from ozone reduction is dependent on the action spectrum used, the steepness of the present latitudinal gradient of solar UV-B irradiance is also quite dependent on the action spectrum used for evaluation.

The effective UV-B radiation for the season of year of maximum solar radiation at different latitudes is shown in Fig. 7. These are plotted relative to the radiation at 40° latitude. (The date of maximum solar radiation at each latitude corresponds to the time when solar zenith angles are minimal. Above 23° latitude this occurs at the summer solstice, but at latitudes less than 23°, this time is progressively closer to the equinoxes, about March 21 and September 23, which are the dates of maximum solar radiation at the equator.) Three different action spectra have been used as weighting functions to illustrate the dependence of this gradient on action spectrum characteristics. Just as the RAF is greater for steeper action spectra (Fig. 6), steeper action spectra also result in a more pronounced latitudinal gradient of solar UV-B irradiance.

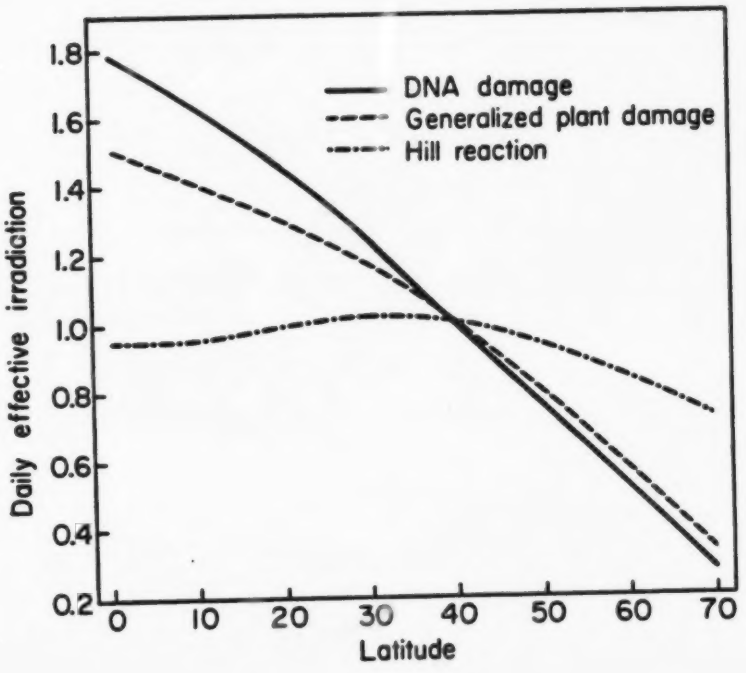

Fig. 7. Daily effective UV-B radiation for the season of year of maximum solar radiation at different latitudes relative to that at 40° latitude calculated according to the generalized DNA damage action spectrum (Setlow 1974), the generalized plant damage action spectrum (Caldwell 1971) and the Hill reaction inhibition spectrum (Jones and Kok, 1966).

If a spectrum has a rather slow rate of decline with increasing wavelength, such as the Hill reaction spectrum, there is no latitudinal solar UV-B gradient. Thus, study of characteristics of plants that have originated from different latitudes can provide some indirect evidence of the type of UV damage action spectrum that is indeed appropriate for plants. For example, if a spectrum such as the Hill reaction is indeed representative of the spectrum for UV damage to plants, one might expect little correlation between the latitude of origin of plants and their sensitivity to UV-B radiation when this radiation is presented at sufficient flux densities to result in damage.

There are several lines of evidence that suggest that a sufficiently steep action spectrum for plant damage exists so that an appreciable latitudinal gradient of solar UV-B radiation has been extant. The first line of evidence is a correlation between the latitude of origin of crop species and their sensitivity to UV-B radiation as measured by a reduction of plant biomass in experiments with UV-B radiation lamps. Over 50% of the crop species which have originated from temperate latitudes were sensitive to UV-B radiation in these tests, whereas for crop species that have originated at low latitudes, only 20% were classified as sensitive (Teramura and Caldwell, unpublished).

The second two lines of evidence are derived from a latitudinal gradient in the arctic-alpine life zone ranging from sea level locations in the Arctic to alpine elevations (3000-4000 m) at mid to low latitudes. In this situation an even steeper gradient should be expected because elevation above sea level is superimposed on the latitudinal gradient (Caldwell et al. 1980). A survey of UV optical properties of leaves from nonagricultural, as well as agricultural, plant species has been conducted by sampling plants in the field at various locations along this gradient and determining the UV epidermal transmittance of the leaves. Plants occurring in areas of high solar UV-B radiation, at low latitudes and high altitudes, exhibited a greater capacity to selectively absorb UV-B radiation in the upper tissue layers of the leaves (Robberecht et al. 1980). If the selective pressure for UV absorption in the epidermis of plant leaves were approximately the same at all locations along this gradient, such as would be the case if an action spectrum like that of the Hill reaction inhibition were appropriate for UV-B damage, one would not expect a correlation between latitude and UV-B filtration capacity of the leaf epidermis.

A third line of evidence involves the inherent differences in sensitivity of the photosynthetic system to UV-B radiation damage that have been demonstrated for species of the same genus or even races of the same species which occur in different locations on the latitudinal gradient of the arctic-alpine life zone (Caldwell et al. 1982). In these experiments, plants were cultured under identical conditions in environmental growth chambers before the sensitivity of their photosynthetic systems to the UV-B radiation was assessed. Arctic races or species consistently showed much greater sensitivity to UV-B radiation and this could not be solely attributed to differences in the optical properties of the leaf epidermis. Such evidence certainly supports the notion that a steeper action spectrum for photosynthetic damage by UV radiation such as that developed using polychromatic radiation (Fig. 4) would be more appropriate than an action spectrum such as that for the Hill reaction. Although all three lines of evidence are circumstantial, they support the notion that an appreciable RAF exists for higher plants.

Biological Assessments and Errors Deriving from Action Spectra

Before radiation amplification factors can be used in assessment of biological and ecological consequences of ozone reduction, it is necessary to demonstrate biological effects of UV-B radiation. Ideally, one should establish a dose-response relationship. In any case, it is at least necessary to show a meaningful response at UV-B flux densities exceeding those currently in sunlight. (Investigations involving the removal of UV-B from solar radiation, such as with filters, have generally not resulted in significant plant responses (Caldwell 1968; Becwar et al. 1982; Caldwell 1981), although there are some notable exceptions (e.g., Bogenreider and Klein 1977).)

Experiments with lamps: One cannot easily simulate the solar spectral irradiance either with or without reduced ozone using UV lamps. Thus, weighted UV irradiance from the lamp system is compared with weighted solar UV irradiance as would occur with a particular solar angle, ozone concentration, etc. The most common lamps used are fluorescent lamps which emit principally in the UV-B region. The spectral irradiance from the most frequently used bulbs is shown in Fig. 8. As with all fluorescent lamps, these are basically low pressure mercury vapor lamps with a phosphor that fluoresces in a continuous spectrum -- in this case, mainly in the UV-B region, but some UV-C and UV-A radiation is included. Though most of the radiant emission from the bulbs comes from the fluorescing phosphor, the emission from the mercury vapor is also present and this appears as distinct lines in the spectrum. The fluorescent lamp manufactured by Philips Co. emits substantially more than the bulb of Westinghouse.

Filters are commonly employed to absorb the UV-C and short-wavelength UV-B radiation emitted by these bulbs. Investigators in Europe have commonly used the Philips bulbs with glass cutoff absorption filters (Schott WG series) for this purpose, while in North America, cellulose acetate plastic film has been used with the bulbs manufactured by Westinghouse (Caldwell et al. 1983). The glass absorption filters have the advantage of being stable in their transmittance, while the plastic film filters are considerably less expensive but exhibit decreased transmittance as they are exposed to UV radiation (Caldwell et al. 1983). The spectral irradiance from filtered and unfiltered lamps shown in Fig. 8 is provided as a comparison of these lamp and filter combinations. Naturally, individual lamps will vary in their emission and, as with all fluorescent lamps, their emission will decrease with age, especially during the first 100 hours of use, and with temperatures that are too warm or too cold for optimal operation (Bickford and Dunn 1972).

If filtered fluorescent lamps are the only source of UV radiation for plant experiments, the discrepancy between spectral irradiance received from the sun and that received from the lamps is considerable (Fig. 9a). When compared with the midday solar irradiance in the summer at temperate latitudes, a bank of filtered Westinghouse fluorescent lamps provide more shortwave UV-B radiation and more than an order of magnitude less longwave UV-B and UV-A radiation. Thus, the action spectrum used to weight the spectral irradiance for comparison of the lamp systems with solar radiation is particularly critical as will be demonstrated subsequently.

When such lamp systems are used to supplement the normal solar radiation, i.e., when plants are exposed both to the solar radiation as well as a

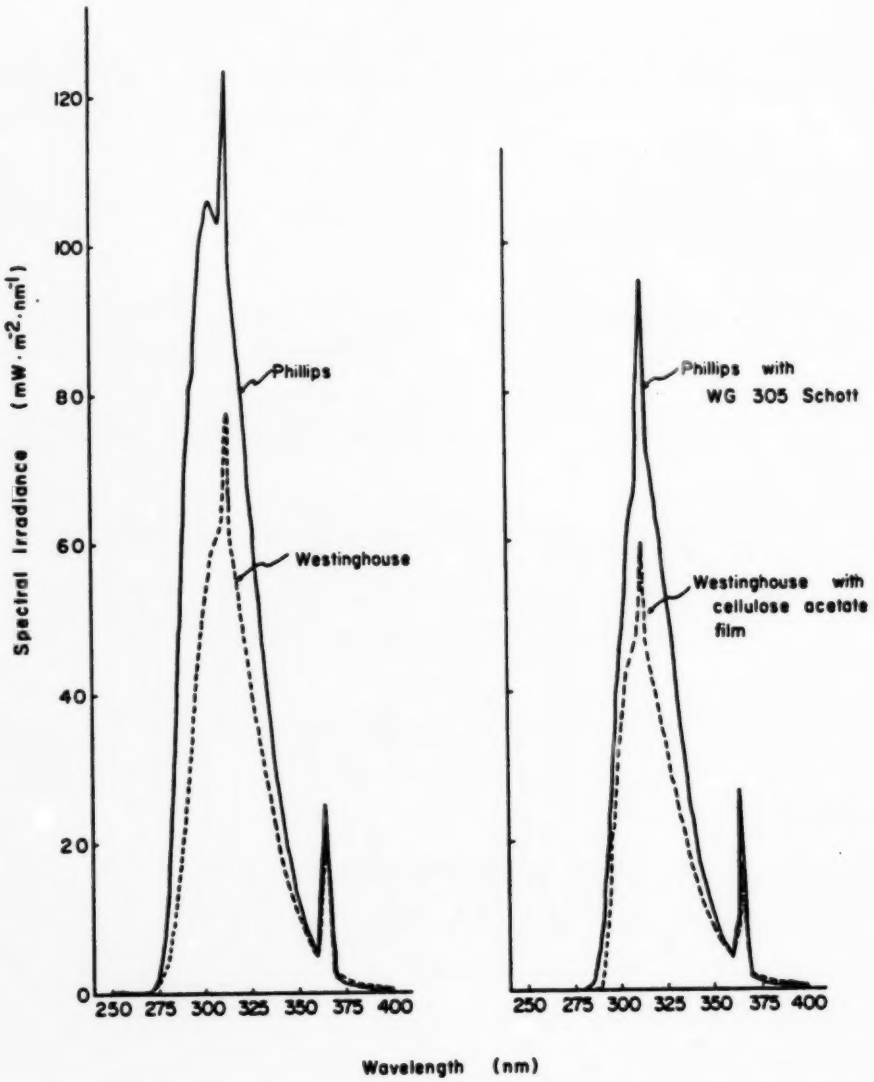

Fig. 8. The spectral irradiance at 30 cm from common fluorescent UV-B lamps with and without filters. The lamps and filters were new and the spectral irradiance was measured with a double monochromator spectroradiometer (Optronic Laboratories). The Philips TL 40W/12 and the Westinghouse FS40 lamps without filters are shown on the left and with filters on the right. Schott WG 305 sharp cutoff absorption filters (2-mm thickness) were used with the Philips lamp and cellulose acetate plastic film (0.13-mm thickness) with the Westinghouse lamp. These lamp/filter combinations have commonly been used in studies in Europe and North America, respectively.

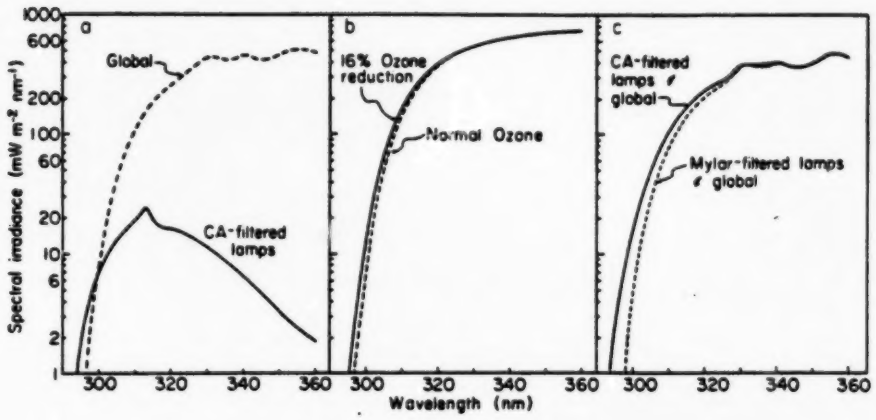

Fig. 9. Global (direct beam + diffuse) UV spectral irradiance and the spectral irradiance from filtered lamp systems used in experiments. In the left panel, a, global spectral irradiance as measured at solar noon on August 20 at 41°45' N latitude and 1460 m elevation and the spectral irradiance from Westinghouse FS40 lamps with cellulose acetate film filters (without background global radiation) are shown. The lamp system is adjusted to provide a UV-B supplement equivalent to a 16% ozone reduction under these conditions calculated according to the generalized plant damage action spectrum. In the middle panel, b, the theoretical global UV spectral irradiance for these conditions, as calculated by the model of Green et al. (1980), is shown for current ozone conditions as well as conditions with a 16% reduction of the atmospheric ozone layer. In the right panel, c, the UV spectral irradiance measured under lamp systems with cellulose acetate and Mylar film filters with the background global radiation is shown. The Mylar-filtered lamp system provides a control with the same UV-A irradiance and obstruction of global radiation as the CA-filtered lamps which constitute the enhancement treatment. The UV-A irradiance in both treatment and control is less than the ambient global shown in the left panel because of the obstruction created by the lamps. The UV-B supplement in the right panel represents the same effective UV-B radiation as that predicted with the Green et al. (1980) model when calculated using the generalized plant damage action spectrum. Adapted from Caldwell et al. (1983).

supplement from the filtered lamp bank, the discrepancy in spectral distribution is much less. Ideally, the supplemented UV spectral irradiance would only be that shown as the difference between solar spectral irradiance under normal conditions and with ozone reduction (Fig. 9b). Since the filtered fluorescent lamps emit longer wavelength radiation than is desired for the supplement, it is necessary to use control lamps which are identical except that they are filtered so as to exclude the UV-B radiation. Thus, the amount of UV-A radiation provided by the control lamps would be the same as that coming from the treatment lamps, and the other microenvironmental influences such as shading by the lamps would also

be the same. In Fig. 9c the resulting spectral irradiance under lamp banks with two different plastic film filters, corresponding to treatment and control, is shown with the solar radiation background. The difference between these is still not a perfect simulation of what would be calculated as the difference between solar spectral irradiance with and without ozone reduction; however, the correspondence is considerably better than when the lamps are used by themselves such as would be the case in a glasshouse, growth chamber or laboratory situation.

Error analysis: There are then two basic types of error that are involved in use of action spectra as weighting functions in biological assessments of ozone reduction, namely RAF errors and enhancement errors. The RAF errors are those resulting from an overestimation or underestimation of the radiation amplification factors by assuming an incorrect action spectrum. The RAF errors would be associated with application of dose-response relationships to the solar UV-B irradiance that would result from various scenarios of ozone reduction. For example, if a given amount of UV-B irradiation corresponding to 10% ozone reduction resulted in 5% reduction of photosynthesis, one would employ the RAF to extrapolate to other ozone reduction levels for a given latitude and season of year.

The enhancement error is that associated with relating UV-B radiation supplied by lamp systems in an experiment with solar UV-B radiation for a particular ozone level. For example, if one desires to provide a UV-B radiation supplement under field conditions corresponding to a 15% ozone reduction, and an incorrect action spectrum is used as a weighting factor for comparing UV irradiance from the lamps and the sun, an error in the desired enhancement will result. The enhancement error necessarily includes an RAF error — namely that associated with calculating the effective UV irradiance corresponding to the 15% ozone reduction.

These two types of error are shown in Fig. 10 for a scenario in which the generalized plant damage action spectrum (Fig. 5) is employed for calculating the RAF and the effective UV radiation enhancement when the DNA-damage spectrum (Fig. 5) is indeed the most appropriate for plant damage. (This is, of course, hypothetical as the most appropriate action spectrum to represent higher plant damage is not known.) The discrepancy between RAF values calculated by the generalized plant damage and DNA damage spectra is illustrated in the upper portion of Fig. 10. With greater ozone reduction, which requires larger RAF values, the divergence from the diagonal 1:1 line increases, i.e., the difference between the RAF values calculated using the two action spectra increases. This is directly from information presented in Fig. 6. The differences in UV radiation enhancement in a field experiment that would result from use of the two action spectra are shown in the lower half of Fig. 10. In field experiments the lamps are used to supplement the solar radiation, and a certain amount of obstruction of the solar global (direct beam + diffuse) radiation inevitably results. The exact spectral distribution of the radiation reaching the plants in the enhancement experiments then depends on the mixture of global and lamp radiation. The relationship in Fig. 10 was determined from actual measurements of spectral irradiance under lamp systems in a field experiment. Each point represents a combination of the UV radiation from the lamps and the background global radiation convoluted using the two action spectra. Relative enhancement is the ratio of the UV-B radiation from the lamps plus the background global radiation to the ambient global radiation without the lamp systems for particular conditions. The range of values shown in

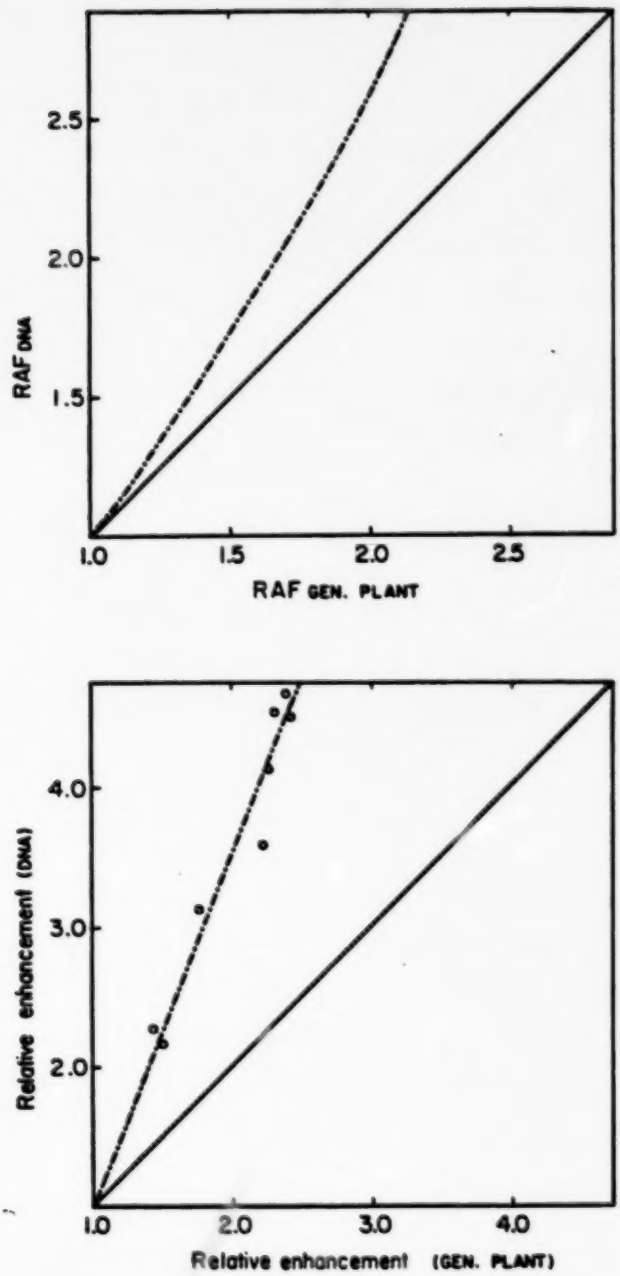

Fig. 10. The relationship between radiation amplification factors calculated with the generalized plant damage action spectrum and the generalized DNA damage action spectrum for different conditions and levels of ozone reduction (upper). The relative enhanced UV-B radiation in field experiments calculated according to the generalized plant damage spectrum and the generalized DNA damage spectrum for different conditions and levels of ozone reduction based on field spectral irradiance measurements (lower). The solid diagonal lines in both graphs represent a situation of equivalence for the RAF and relative enhancements calculated from the two spectra.

Fig. 10 results from different experiments in which enhancements corresponding with different levels of ozone reduction and different solar angles were used. The lamp system is specially modulated so that the amount of UV supplement is adjusted for particular solar conditions such as solar angle, atmospheric turbidity, current ozone concentrations, etc. (Caldwell et al. 1983). A linear regression fits these points adequately ($r^2 = 0.96$). The discrepancy between relative enhancements calculated by the two action spectra is greater than the discrepancy between the RAF values calculated with the two spectra.

For the action spectra represented in this paper (Figs. 1, 4 and 5) and the filtered UV fluorescent lamps commonly used, (Fig. 8), the RAF and enhancement errors are in opposite directions as depicted in Fig. 11. These relative errors are shown as a function of ozone reduction for field enhancement experiments under temperate-latitude conditions in the summer as portrayed in Fig. 10. The scenario is the same, namely, that the generalized plant damage action spectrum was assumed while the DNA-damage spectrum is correct. Although the relative RAF errors are small for situations where the ozone reduction is small, this is not the case for the enhancement errors (Fig. 11).

If a different scenario is pursued such that the generalized plant damage spectrum is assumed, but a spectrum with a slower rate of decline with increasing wavelength, such as the R-B spectrum (Fig. 5), is correct, then the RAF and enhancement errors would be reversed—an overestimation of the RAF and underestimation of the enhancement.

As shown in Fig. 9, field UV enhancement experiments provide a much closer simulation of the spectral irradiance resulting from ozone reduction than do experiments in glasshouses or growth chambers in which UV radiation is provided only by filtered fluorescent lamps, since there is no solar UV background. The enhancement errors that might result from use of an incorrect action spectrum for calculating the enhancement are considerably greater than for field experiments, as shown in Fig. 12. The spectral irradiance from filtered Philips and Westinghouse UV fluorescent tubes following aging of the lamps and filters for about 100 hours was used to calculate the errors shown in Fig. 12. The same spectral distribution is assumed for all enhancement levels in such experiments, which is normally the situation, as doses are typically adjusted by varying the number of lamps, distance between the lamps and the experimental objects, or use of neutral density filters. The errors portrayed here are striking, especially when one considers that the two action spectra used for this scenario are not so very dissimilar (Fig. 5). Other scenarios could easily lead to larger overestimation or underestimation errors for the calculated enhancement. Also, for the errors depicted in Fig. 12 the relative overestimation errors are greater at UV levels corresponding to smaller ozone reductions.

If a source of background UV radiation were present, such as from a xenon arc lamp, these errors could be substantially reduced. However, this would depend on the flux density and spectral distribution received from the background source. An empirical analysis of the errors for particular situations would need to be conducted. However, without knowledge of the most appropriate action spectra for plant damage, the error analysis remains as a heuristic exercise quite dependent on the action spectrum scenarios assumed.

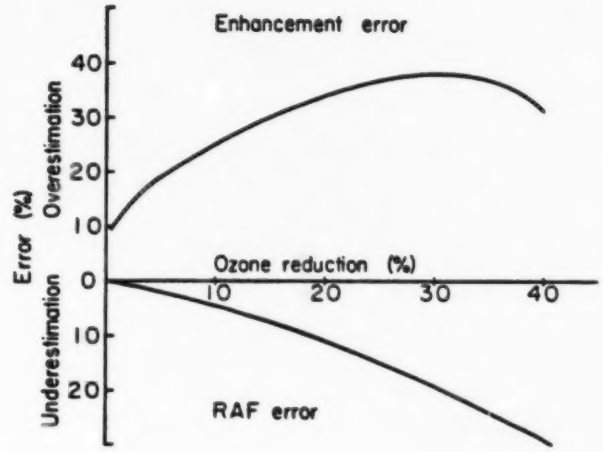

Fig. 11. Relative RAF and enhancement errors as a function of ozone reduction for field UV supplementation experiments under temperate-latitude conditions in the summer as portrayed in Fig. 10. The scenario for these errors is that the RAF values and the enhancements were calculated following the generalized plant action spectrum when the DNA damage spectrum was indeed correct.

CONCLUDING REMARKS

The potential errors resulting from assuming an incorrect action spectrum are compelling reasons for further action spectrum development. This should indeed be pursued. Yet, one should not expect that a single definitive action spectrum for higher plant damage will necessarily be forthcoming. It is unlikely when one considers the many basic modes of damage to plant tissues that UV radiation can effect (Fig. 1), the physiological and morphological diversity of plant species, and the interactions with other environmental factors, such as visible light, that can ensue.

Extrapolation from spectra of component reactions of isolated organelles to spectra of higher plant response in nature is precarious as shown for the case of photosynthetic damage (Fig. 4). Thus, use of intact plant organs and polychromatic radiation should be emphasized in further action spectrum development where these spectra bear on the ozone reduction problem. For damage to higher plant photosynthesis, the provisional action spectrum developed for Rumex patientia (Fig. 4) as well as circumstantial evidence from the natural latitudinal gradient indicate that the appropriate action spectrum is much steeper than the spectra for the Hill reaction. Thus, contrary to what one might conclude from component photosynthetic reactions, an appreciable RAF exists for damage to higher plant photosynthesis. More recent preliminary work with polychromatic radiation suggests that the spectrum may yet be even steeper and, therefore, one should view the Rumex spectrum presented here as only provisional.

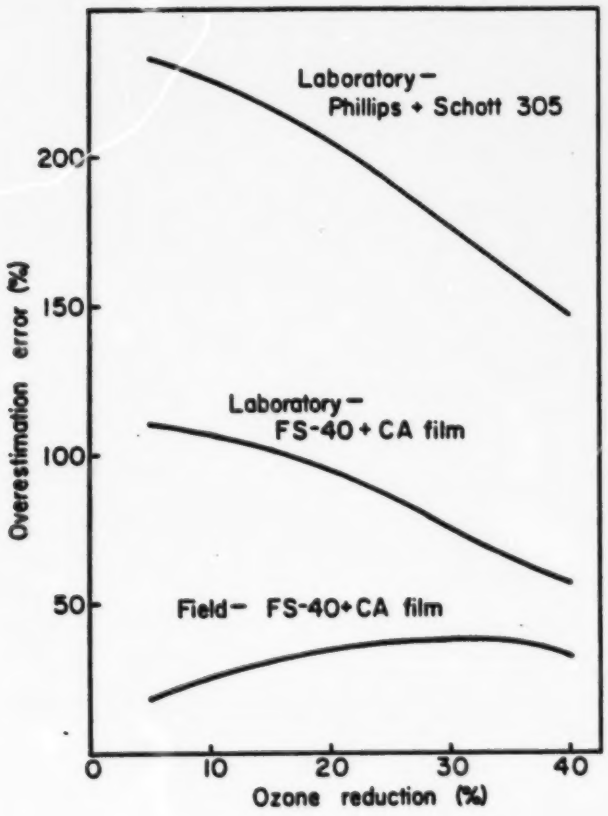

Fig. 12. Enhancement errors calculated according to the same scenario as for Fig. 11, but with enhancement experiments using different lamp systems. In the field supplementation experiment using Westinghouse FS40 lamps and cellulose acetate film, the errors are the same as portrayed in Fig. 11. Under laboratory conditions (which would correspond to glasshouse or growth chamber conditions with no background UV radiation) the Philips lamps with Schott WG 305 filters and the Westinghouse FS40 lamps with cellulose acetate film render the errors depicted. The lamps and filters were aged for about 100 hours for these measurements.

In our present state of ignorance concerning the most appropriate action spectra for higher plant damage, we feel it is reasonable to continue to use an action spectrum with an intermediate rate of decline with increasing wavelength, such as the generalized plant damage spectrum. An intermediate spectrum will, of course, yield intermediate RAF and enhancement values. If the appropriate spectra are later found to be either steeper or flatter, correction from an intermediate spectrum will be easier to conduct.

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